frontiers | Frontiers in Ecology and Evolution

TYPE Original Research
PUBLISHED 08 November 2022
DOI 10.3389/fevo.2022.1018615

Check for updates

OPEN ACCESS

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SPECIALTY SECTION
This article was submitted to Paleoecology, a section of the journal Frontiers in Ecology and Evolution

RECEIVED 13 August 2022
ACCEPTED 10 October 2022
PUBLISHED 08 November 2022

CITATION
Yu C and Cui Y (2022) Body size and age estimation of Chinese sea bass (*Lateolabrax maculatus*) and evidence of Late Neolithic fishing strategies, a case study from the Guye site. *Front. Ecol. Evol.* 10:1018615. doi: 10.3389/fevo.2022.1018615

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Body size and age estimation of Chinese sea bass (*Lateolabrax maculatus*) and evidence of Late Neolithic fishing strategies, a case study from the Guye site

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Fishing was an important form of subsistence economy among ancient societies. However, details of past fishing activities have been rarely studied in China. This paper uses data extracted from a modern fish collection to estimate the body size and age of Chinese sea bass from the Guye site, a common species that is frequently discovered in archaeological sites of coastal South China. The distribution of body size and age were reconstructed and combined with fish biology and ecology; the current dataset revealed that the main fishing grounds of the Late Neolithic Guye people were close to the shoreline, and the main fishing season was from spring to early autumn.

KEYWORDS

body size estimation, age estimation, Chinese sea bass, Guye site, ichthyoarchaeology

Introduction

The reconstruction of fish body size is an important indicator that not only provides crucial information about the size range and distribution of fish size in an ichthyoarchaeological assemblage, but allows further interpretation of past fishing methods, grounds, gears, and seasons (Wheeler and Jones, 1989). Previous ichthyofaunal studies in China focused on the freshwater taxa from the Tianluoshan and Jiahu sites in the Lower Yangtze River region (Nakajima et al., 2011, 2012, 2015, 2019; Matsui et al., 2016; Zhang, 2018; Maruyama et al., 2021). The regression formulas for common carp (*Cyprinus carpio*) and snake head (*Channa argus*) were calculated aiming to look for early aquaculture and rice paddy field management (Zhang, 2018; Nakajima et al., 2019).

However, given that the varied fish species from the Pearl River Delta region of South China are very different from those of the Lower Yangtze River region, it is necessary to select some species of fish to initially develop the use of osteometric measurements as a means of estimating fish body size. This study provides regression formulas for size estimation of Chinese sea bass (*Lateolabrax maculatus*), the most abundant marine species in the Guye site and is also commonly recovered from archaeological sites bordering coastal South China (Yu and Cui, 2021). The present study reveals the patterns of the body size and age of Chinese sea bass that are linked with fishing strategies in coastal South China during the Late Neolithic age, which helps to elucidate the mechanisms of the sustainability and complexity of fishing-hunting-gathering communities in antiquity.

Ichthyological biology and ecology

There has been disagreement on the ichthyological taxonomy of Lateolabrax (Teleostei: Perciformes: Lateolabracidae: Lateolabrax). FishBase (Froese and Pauly, 2022) and the latest version of *Fishes of the World* (Nelson et al., 2016) suggest there are only two species in genus Lateolabrax, namely *L. japonicus* (Japanese sea bass) and *L. latus* (black fin sea bass). However, local ichthyologists argued that *L. maculatus* (Chinese sea bass) and *L. japonicus* are different species based on modern morphology, genetics, ecological habits, and natural distributions (Yokogawa, 1993, 2004, 2019; Yokogawa and Seki, 1995). The Chinese sea bass is characterized by its lifelong black spots on body and dorsal fins although some might gradually downsize with growth, generally they are still larger than the scales (Figure 1). It is broadly distributed along the entire Chinese coast's offshore waters including the Bohai Sea, Yellow Sea, East China Sea, South China Sea, and west coast of the Korean Peninsula (Figure 2) (Feng and Jiang, 1998). Black spots on Japanese sea bass are usually scattered above lateral line on the juvenile individuals and then vanish at 21–25 cm standard length, the spots are about the size of, or smaller than, the scales. This fish is commonly found in the east coast of the Korean Peninsula and Sea of Japan (Yokogawa and Seki, 1995; Yokogawa, 2004). Black fin sea bass have no black spots and are distributed along the entire Japanese coast's offshore waters including the west coast of the Sea of Japan, and the west shores of the Honshu, Shikoku, and Kyushu islands (Katayama, 1957; Overseas fishery cooperation foundation of Japan, 2009; Wu and Zhong, 2021). Although we are unable to distinguish the bone characteristics among them due to the lack of comparative material, the main fisheries in prehistoric coastal South China can be identified as *L. maculatus* according to their modern distribution.

Chinese sea bass is a euryhaline teleost which can live in salinities ranging from freshwater to seawater environments. Some juveniles can survive in freshwater where they grow into adults before migrating back into the ocean to spawn. Chinese sea bass are frequently found in the moving water of rocky reefs when they are inshore. They migrate seasonally, leaving the coast during winter to stay in wintering grounds and spawn, usually in an offshore area; and enter shallow waters near the coast or inside the bay in spring and summer for feeding. The older the fish is, the further they migrate (Feng and Jiang, 1998).

Materials and methods

Modern fish collection

A total of 20 Chinese sea bass were collected at fish markets of coastal China, including Dalian (Liaoning province), Ningbo (Zhejiang province), Guangzhou, and Zhanjiang (Guangdong province) (Figure 2). Body measurements were conducted, including standard length (SL) in millimeters, and the total fresh weight (W) in grams (Figure 1). The Chinese sea bass involved in this study ranged from 116 to 740 mm and from 23 to 5675 g (Table 1). According to Feng and Jiang (1998), this species can reach 817 mm in standard length, which indicates that our collection covered almost the full range of size that this species can attain, although the number of individuals is not

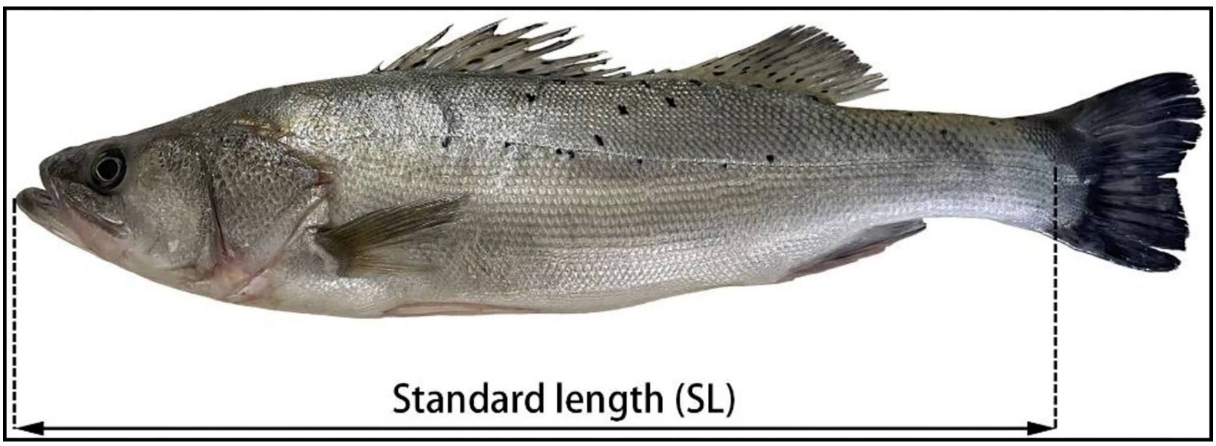

FIGURE 1
Chinese sea bass and measurement illustration of standard length (SL).

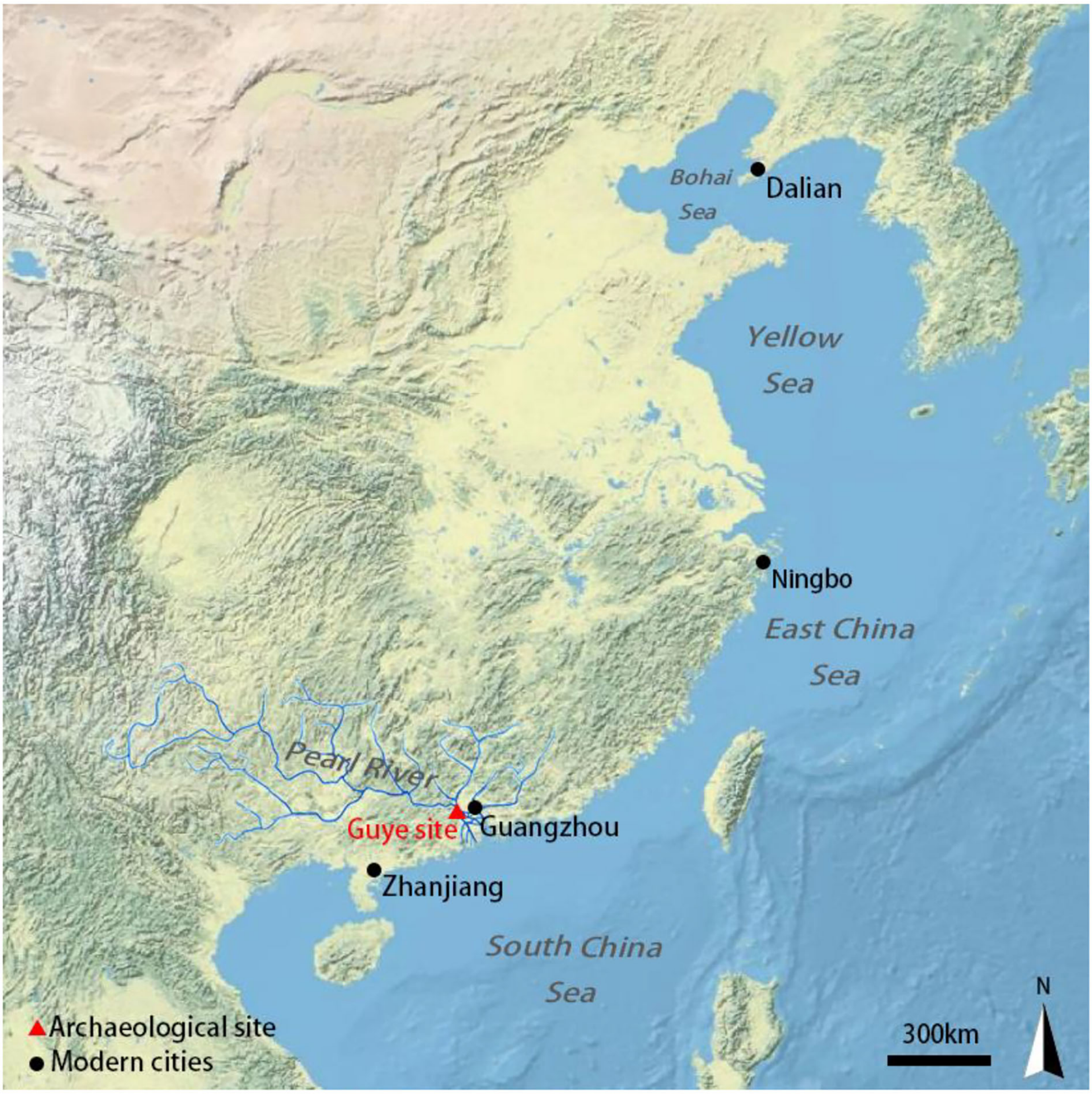

FIGURE 2
Location of the Guye site and the comparative collections.

as great as many similar studies (Yeomans, 2016; Lidour et al., 2018; Martínez-Polanco and Béarez, 2020; Rurua et al., 2020; Martínez-Polanco et al., 2022).

Osteological nomenclature of bones mainly follows Lepiksaar (1994) and Dye and Longenecker (2004). Bone measurements are described in Table 2 and illustrated in Figure 3. All biometric data were taken using a Mitutoyo caliper (precision: tenths of a millimeter) with a precision of two decimal points. The same dimensions of the right and left sides are averaged.

Archaeological samples

The site of Guye (Late Neolithic period, 5,900–5,400 cal. BP) is situated on the west bank of the Pearl River Delta, and was proved to be the earliest shell midden site of the region (Cui, 2007). All the excavated sediments were systematically wet sieved using different sizes of meshes (1.5 and 4 mm). This sampling method provided enormous amounts of faunal remains. Preliminary zooarchaeological investigations have revealed that the subsistence economy of Guye heavily

TABLE 1 Standard length, weight, and location of collection of Chinese sea bass (*Lateolabrax maculatus*) used in this study.

No.	SL (mm)	W (g)	Location of collection
006	330	650	Guangzhou
029	320	594	Guangzhou
035	340	718	Guangzhou
054	310	700	Guangzhou
167	430	1,043	Dalian
202	620	3,605	Ningbo
203	200	162	Ningbo
204	185	128	Ningbo
205	116	23	Ningbo
211	480	165	Zhanjiang
212	490	2,139	Zhanjiang
217	740	5,675	Ningbo
419	592	2,620	Ningbo
420	625	4,270	Ningbo
456	620	3,400	Ningbo
457	535	2,200	Ningbo
458	710	4,250	Ningbo
470	620	2,910	Ningbo
475	437	1,250	Ningbo
476	655	3,910	Ningbo

relied on fishing. Among the whole assemblage, 11,407 fish bones were sorted with a total of 2,452 remains identified to family level or below (i.e., genus, species), making it the first ichthyofaunal dataset from prehistoric populations in coastal South China. Chinese sea bass was the most common marine species, it comprised about 22% of the total NISP and MNI (Yu and Cui, 2021).

The calculation of regression formulas

The calculation of regression formulas for Chinese sea bass was based on a set of modern fish collected with known length and weight (Table 1). Clear dimensions shown on Figure 3 were used to generate length-length and length-weight equations represented by $Y = aX^b$ whereas Y is the standard length and weight of the fish, respectively, X is the measurement of the representative dimension from the modern collection. The quality of the relationship is given by the coefficient of determination (R^2) which ranges from 0 to 1. The value of R^2 shows whether the model would be a good fit for the given data set. Generally, a higher coefficient indicates a better fit for the model. With good coefficient of determination, the functions can be used to estimate the length and the weight of the fish from its isolated bones.

Result

Length-weight equation

A standard length-weight model was obtained in the form $W = aSL^b$, with the W in grams and the SL in millimeters. The standard length-weight relationships reflected a slight allometric growth (b = 2.815), with a high coefficient of determination ($R^2 = 0.9879$) (Figure 4).

Bones measurements and regression analysis

Equations are given in the form $SL_{fish} = aM^b_{bone}$, where all the measurements are taken and calculated in millimeters. The a and b parameters and R^2 are provided in Table 3. All of the equations show a good coefficient of determination; the maximal R^2 is 0.9925, the minimal R^2 is 0.9591, with an average of 0.9803. The correlations of the preopercle measurements ($R^2_{M1} = 0.9909$; $R^2_{M2} = 0.9887$; $R^2_{AVG} = 0.9898$) are very good. Followed by hyomandibular ($R^2_{M1} = 0.9888$; $R^2_{M2} = 0.9904$; $R^2_{AVG} = 0.9896$). The measurements of maxilla provide the lowest coefficients, still superior to 0.967, however.

Ichthyoarchaeological application

The ichthyoarchaeological application of regression formulas needs a set of measurements from frequent and well-preserved bones in the archaeological assemblages. According to the distribution of fish skeletal parts from the Guye site, the most frequently recovered element of Chinese sea bass is the opercle (Table 4), which is diagnostic with its thickness and pointedness at the posterior end. However, the opercle is very porous as seen from the cross section, which might be the cause of high fragmentation of this element, and therefore it lacks measurable dimension. The anterior of the dentary is very robust and the three oval openings on the outer surface make it easy to identify (Yu, 2022). Thus, the anterior height of the dentary (Den M1) was selected for the reconstruction of body length, due to its high correlation coefficient and frequency ($R^2 = 0.9729$) of corresponding bones in the archaeological contexts (Figure 5).

In total, 70 measurements of Den M1 were collected from the Guye assemblage, the minimal reconstructed length was 148.47 mm (SL) and the maximum was 728.7 mm (SL), which gave a mean of 417.79 mm (SL) and a median of 433.18 mm (SL). The main size class represented was 250–550 mm (N = 51; 72.86% of the total population) (Figure 6).

TABLE 2 Descriptions of the bone measurements taken from Chinese sea bass (*Lateolabrax maculatus*) skeletons.

Measurements	Abbreviation	Description
Vomer M1	Vom M1	Maximal mediolateral width of the vomer
Basioccipital M1	Boc M1	Maximal width of the articular surface of the basioccipital
Basioccipital M2	Boc M2	Maximal height of the articular surface of the basioccipital
Premaxilla M1	Pmx M1	Maximal length of the ascending process of the premaxilla
Premaxilla M2	Pmx M2	Maximal length of the premaxilla, from the rostral tip to the tip of the caudal process
Premaxilla M3	Pmx M3	Thickness of the tooth plate
Maxilla M1	Mx M1	Distance between the dorsal condyle and the ventral tips of the external and internal processes
Maxilla M2	Mx M2	Maximal width of the dorsal condyle
Maxilla M3	Mx M3	Maximal length of the maxilla, from the rostral tip of the external process to the tip of the caudal processes
Dentary M1	Den M1	Anterior height of the dentary
Dentary M2	Den M2	Maximal height, between the coronoid and the ventral processes
Dentary M3	Den M3	Maximal length, from the rostral tip of the dentary to the caudal tips of the coronoid and ventral processes
Articular M1	Art M1	Maximal length, between posterior ventralis angulus and the anterior process
Articular M2	Art M2	Maximal height, between the coronoid processes and anterior ventralis angulus
Articular M3	Art M3	Maximal width of the quadrate facet
Quadrate M1	Qd M1	Distance between the external tip of the lateral condyle and the internal tip of the mesial condyle
Quadrate M2	Qd M2	Distance between the ventral tip of the mesial condyle and the dorsal tip of the ectopterygoid margin
Quadrate M3	Qd M3	Distance between the tip of the mesial condyle and the tip of the preopercular process
Palatine M1	Pal M1	Maximal length of the palatine
Hyomandibular M1	Hm M1	Distance between the sphenotic facet and the opercular process
Hyomandibular M2	Hm M2	Distance between the symplectic facet and the line joining the tips of the sphenotic and pterotic facets
Opercle M1	Op M1	Maximal height of opercle
Opercle M2	Op M2	Maximal width, from the articular fossa to the tip of the posterior angulus
Preopercle M1	Pop M1	Maximal length of the preopercle
Preopercle M2	Pop M2	Maximal height of the preopercle
Post-temporal M1	Ptp M1	Distance between the tips of the two processes
Post-temporal M2	Ptp M2	Distance between ventral process tip and posterior tip
Post-temporal M3	Ptp M3	Distance between dorsal process tip and posterior tip
First vertebra M1	FV M1	Maximal width of the exoccipital articular surface
First vertebra M2	FV M2	Maximal height of the vertebra
First vertebra M3	FV M3	Maximal height of the centrum (cranial side)
First vertebra M4	FV M4	Maximal width of the centrum (cranial side)
First vertebra M5	FV M5	Maximal width between the lateral processes (cranial side)
Sagitta M1	Sag M1	Maximal length (rostro-caudal axis)
Sagitta M2	Sag M2	Maximal height (dorso-ventral axis)
Cleithrum M1	Cl M1	Maximal length of the cleithrum
Cleithrum M2	Cl M2	Distance between the tip of the anterodorsal process and the scapula joint

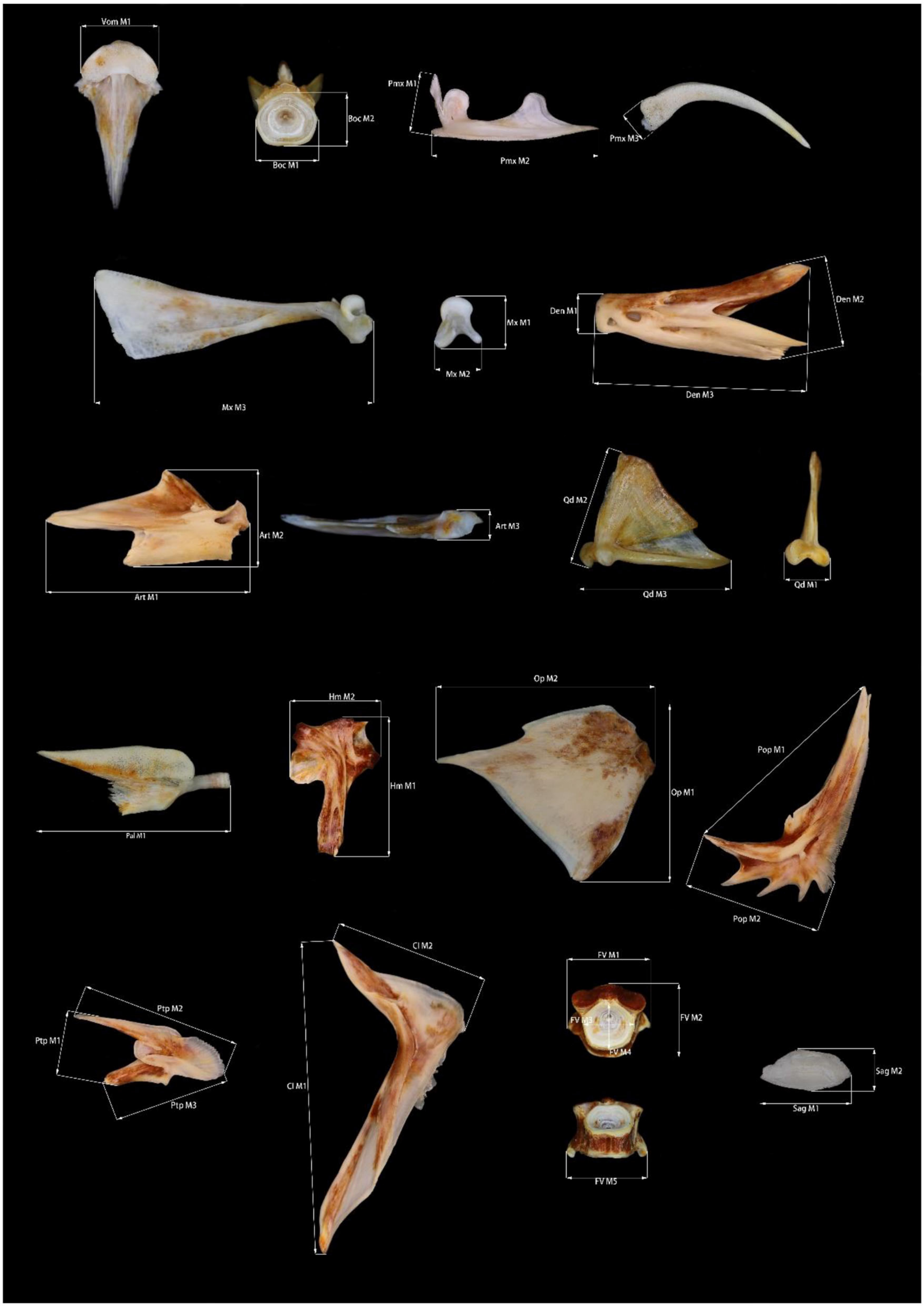

FIGURE 3
Position of the osteological measurements taken from Chinese sea bass.

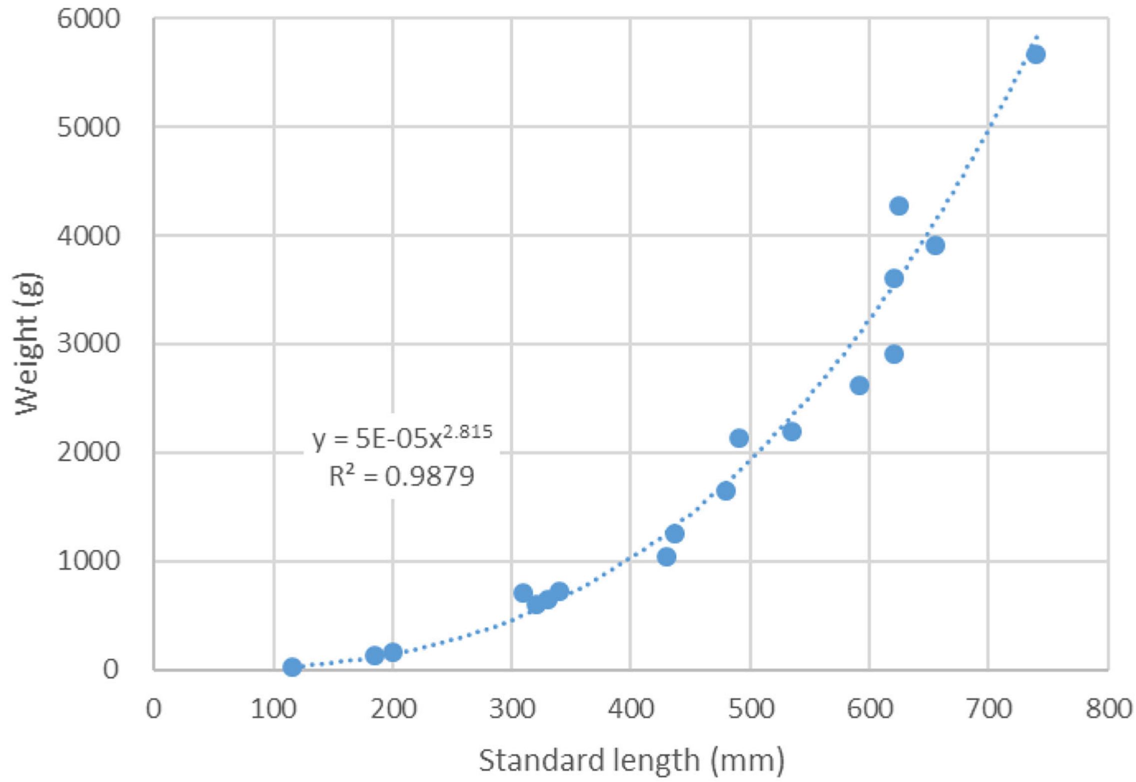

FIGURE 4
Standard length (SL) to weight (W) relationship of the modern sample of *Lateolabrax maculatus*.

Discussion and interpretation

Length–age relation

Growth in fish is indeterminate, which means growth continues throughout the life span of an individual, although at a constantly decelerating rate. Hence older animals are generally larger (Helfman et al., 2009). To estimate the age of Chinese sea bass, we used data collected from 528 individuals from the north Yellow Sea and Bohai Sea by Feng and Jiang (1998) to generate an age-length equation (Figure 7). We then applied estimated body length by dentary anterior height to calculate age for each individual.

It is obvious that the proportion of individuals caught at an age <1 year-old is quite small (4.48%), while 65.67 % of the sea bass were caught between 1 and 3 years of age, 14.93% of the corpus were consumed around 3–4 years-old and same proportion for individuals older than 4 years of age (Figure 8). As Chinese sea bass were sexually mature around 3 years old (Feng and Jiang, 1998), this means that <30% of the catches were mature individuals.

Seasonality evidence and fishing strategies

In the fish assemblages of the Guye site, Chinese sea bass and mullet were the most common marine species. About 17% of the total NISP and MNI belong to Mugilidae, represented by opercle, dentary, lachrymal, and vertebrae. However, it is difficult to differentiate them to the genus level due to similar morphological appearances, especially in archaeological contexts. Based on their body size in modern fishery records, we assumed that mullets in the corpus probably belong to *Liza haematocheilus* (redlip mullet) or *Mugil cephalus* (striped mullet) (Yu and Cui, 2021).

Redlip mullet inhabit shallow coastal waters; they can also enter freshwater regions of rivers. They migrate offshore in the winter and move back inshore in spring for feeding and spawning. Striped mullet are frequently found coastally in estuaries and freshwater environments and inhabit sandy or muddy bottoms. Adults form huge schools and migrate offshore in large aggregations during fall and spawn during winter. Parent fish and larvae migrate back inshore to the feeding

TABLE 3 Regression formula parameters for estimating the total length of Chinese sea bass (*Lateolabrax maculatus*) from bone measurements (in mm).

Measurements	a	b	R^2	N
Vomer M1	32.363	1.0347	0.9795	17
Basioccipital M1	52.558	0.9497	0.9834	18
Basioccipital M2	57.968	0.992	0.9773	18
Premaxilla M1	25.109	1.134	0.9648	20
Premaxilla M2	7.5645	1.1416	0.9828	20
Premaxilla M3	61.087	1.066	0.9722	20
Maxilla M1	53.062	1.0568	0.9606	20
Maxilla M2	36.416	1.2029	0.9607	20
Maxilla M3	7.0716	1.0722	0.9796	20
Dentary M1	58.369	0.954	0.9729	18
Dentary M2	20.826	1.0152	0.9744	20
Dentary M3	6.9928	1.0843	0.9806	20
Articular M1	6.2663	1.11	0.9837	20
Articular M2	19.631	1.0169	0.9791	20
Articular M3	83.009	0.92	0.9591	20
Quadrate M1	67.341	0.9926	0.9749	20
Quadrate M2	18.46	1.0646	0.9849	20
Quadrate M3	13.263	1.0909	0.9908	20
Palatine M1	8.082	1.1539	0.9832	20
Hyomandibular M1	9.5926	1.1009	0.9888	20
Hyomandibular M2	19.569	1.0205	0.9904	20
Opercle M1	7.1141	1.0784	0.9883	20
Opercle M2	13.713	0.8861	0.9754	20
Preopercle M1	6.1935	1.0859	0.9909	20
Preopercle M2	9.6735	1.1153	0.9887	20
Post-temporal M1	21.256	1.1385	0.9832	20
Post-temporal M2	12.914	1.026	0.9925	20
Post-temporal M3	20.333	0.9728	0.9883	20
First vertebra M1	31.457	1.0049	0.9828	19
First vertebra M2	42.394	0.9708	0.9891	19
First vertebra M3	49.368	1.0331	0.9799	19
First vertebra M4	50.137	0.9613	0.9866	19
First vertebra M5	35.055	0.9443	0.9852	19
Cleithrum M1	3.9189	1.091	0.9904	20
Cleithrum M2	11.544	1.0182	0.9782	20
Sagitta M1	10.427	1.3363	0.9799	18
Sagitta M2	19.457	1.5234	0.9679	18

TABLE 4 Distribution of Chinese sea bass skeletal parts at the Guye site (in descending order of NISP).

Skeletal parts	NISP	NISP %
Opercle	167	37.70
Dentary	89	20.09
Articular	55	12.42
Premaxilla	52	11.74
Preopercle	30	6.77
Cleithrum	27	6.09
Hyomandibular	7	1.58
Palatine	5	1.13
Ceratohyal	4	0.90
Post-temporal	3	0.68
Pharyngeal bone	2	0.45
Urohyal	2	0.45
Total	443	100.00

ground in spring and summer times. Striped mullet move into deeper waters as they grow (Zhao et al., 2016). Because we are unable to identify those mullets to genus or species, it is not possible to reconstruct their body size. However, their migratory patterns are almost the same as Chinese sea bass, that is, offshore during winter and inshore during spring and summer.

Fishing methods in nearshore and offshore water areas are different in the modern marine fishery. Mid-water or bottom trawl and purse net are commonly used in offshore water together with advanced fishing boats, particularly during winter (Yang, 2007). In the Guye site, Chinese sea bass and mullet comprised about two-thirds of the total marine species (both NISP and MNI) (Yu and Cui, 2021). If we assume that large-scale fishing activities in offshore water during winter in the Late Neolithic period is rare, then most of the marine fish were caught when winter migration ended, during spring, summer, and early autumn in nearshore and bay areas.

Conclusion

This study, for the first time, provides regression formulas for size estimation of fish species from the coastal South China area. Measurements taken on bones of modern Chinese sea bass enable us to reconstruct the body size of fish discovered in archaeological sites. Based on the length-age equation, the majority of Chinese sea bass collected from the Guye site ranged from 250 to 550 mm and aged from 1 to 3 years old. Based on fish biology and ecology, the cluster of these individuals indicates a fishing ground close to the shoreline. In conjunction with evidence on the characteristics of migration patterns from mullet, the main fishing seasons could be ranged from spring to early autumn.

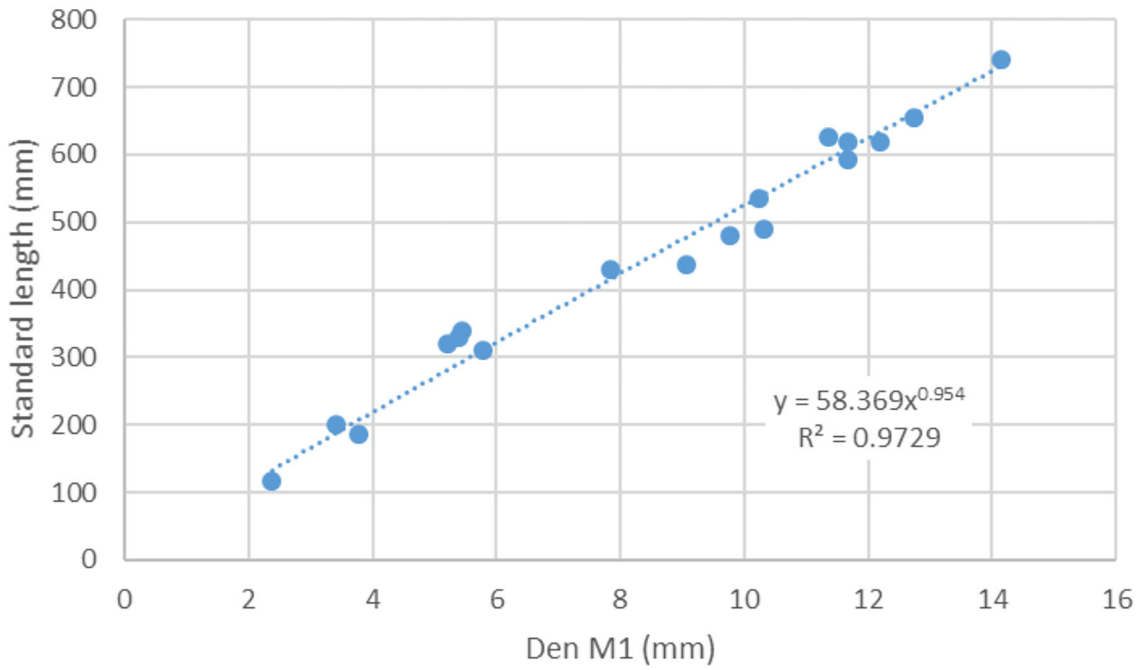

FIGURE 5
Lateolabrax maculatus graph modeling the regression formulas of Den M1 vs. SL.

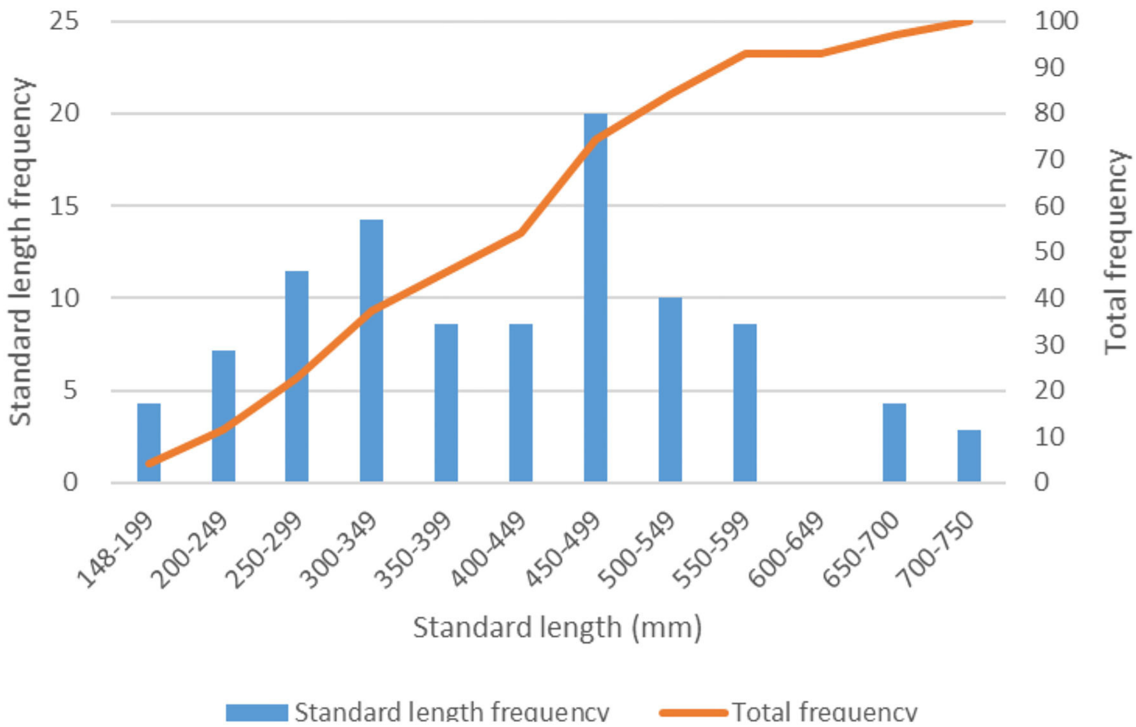

FIGURE 6
Estimated standard lengths of Chinese sea bass of Guye site, $N = 70$.

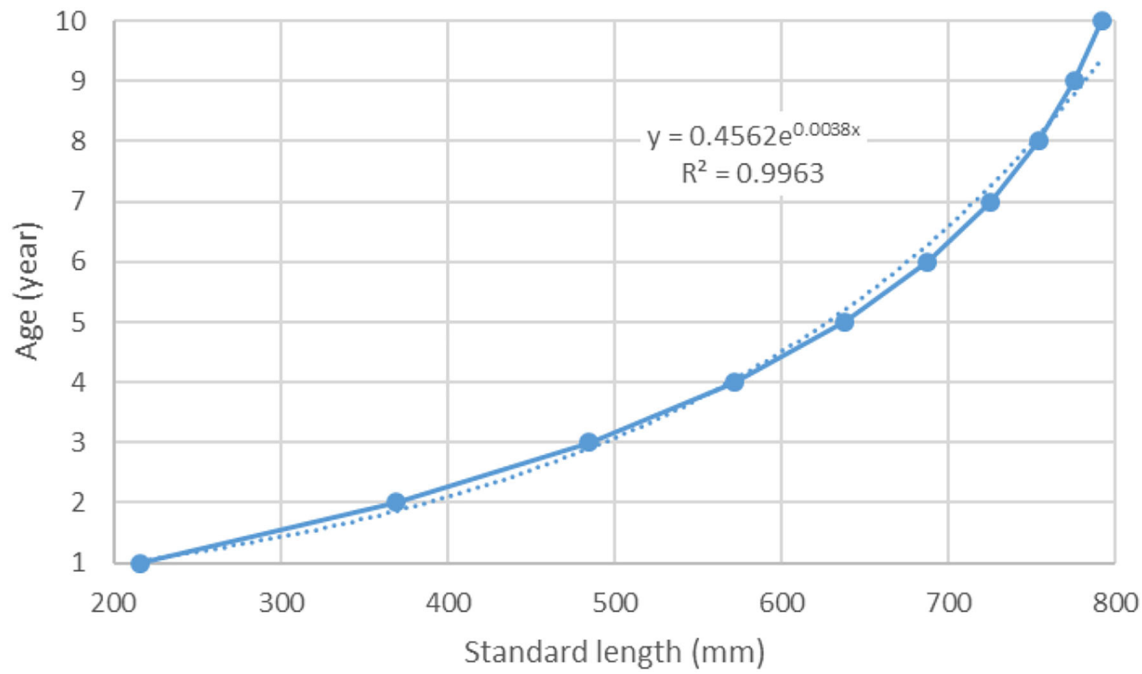

FIGURE 7
Age-length relationship of Chinese sea bass.

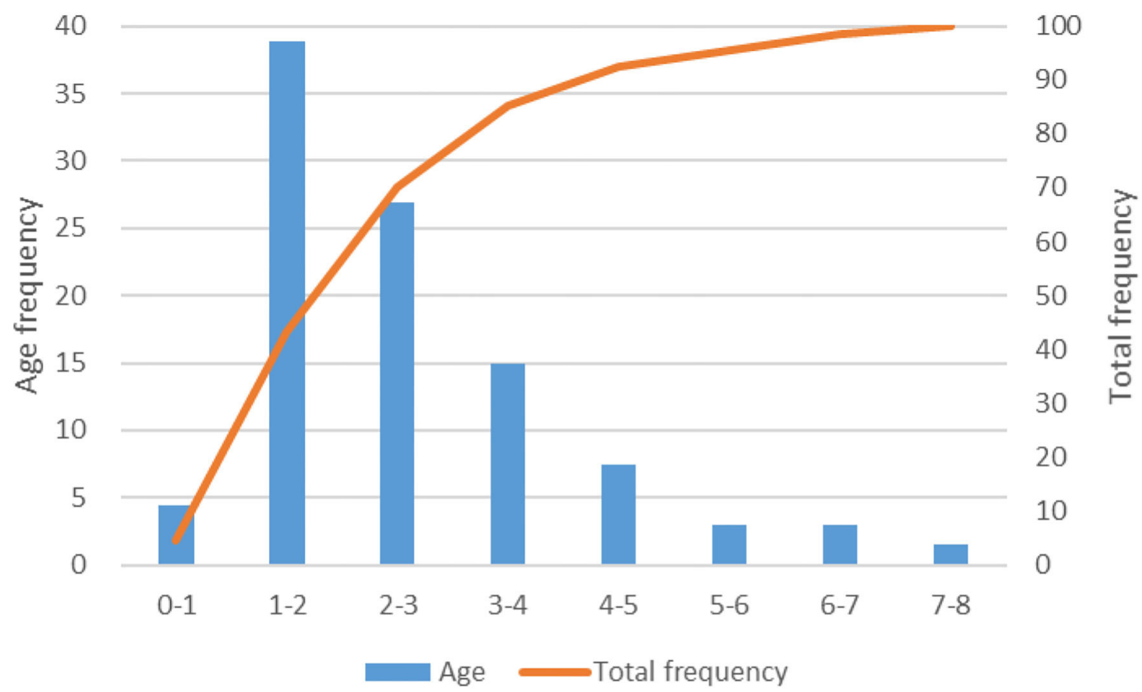

FIGURE 8
Frequency of estimated age classes of archeological Chinese sea bass.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

Ethics statement

Ethical review and approval were not required for the study of animals in accordance with the local legislation and institutional requirements.

Author contributions

CY: conceptualization, methodology, formal analysis, data curation, funding acquisition, writing—original draft, writing—review, and editing. YC: resources and fieldwork administration. All authors contributed to the article and approved the submitted version.

Funding

This study was supported by the National Social Science Fund of China (Grant No. 18CKG005).

Acknowledgments

We would like to thank Zixian Jiang for her contribution to photo editing. We are also grateful to the reviewers who helped us improve the final version of this paper.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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